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Egg Mass Design Relative to Surface-Parasitizing Parasitoids, with Notes on *Asterocampa clyton* (Lepidoptera: Nymphalidae)

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Abstract. The shape of an egg mass for protection of the greatest percentage of eggs from surface mortality factors, in this case parasitism, is considered using geometrical models. Egg mass design is described in terms of both numbers and stacking pattern of eggs. Egg mass design in *Asterocampa clyton* (Boisduval and Le Conte) (Lepidoptera: Nymphalidae) is compared with design attributes predicted by the models.

Introduction

Many insects deposit their eggs in masses (Hinton, 1981) including some species of butterflies (see Stamp, 1980, for overview). There are advantages to depositing eggs in masses which increase the relative fitness of those females which do so by increasing the survivorship of both the eggs and the larvae over females that do not. Among several possible advantages to clustering eggs from the standpoint of egg survivorship, there is reduction of the egg surface area (percentage of eggs) exposed to mortality factors such as parasitism and dessication. This paper considers egg mass design in response to egg mass parasitoids that attack exposed eggs.

Exposed eggs in a cluster (generally those on the surface) may be concealed in several ways: 1) with scales or accessory gland material (Anderson, 1976; Darling and Johnson, 1982), or 2) by variations in egg mass shape, which controls the percentage of eggs exposed. The degree of parasitization is also affected by the size of egg masses and their rate of discovery and utilization by parasitoids. Smaller egg masses of the gypsy moth, *Lymantria dispar* (L.), are more heavily parasitized than larger egg masses, owing to both the stacking design (shape) and number of eggs (Brown and Cameron, 1979, 1982; Crossman, 1925; Dowden, 1961; Hoy, 1976; Weseloh, 1972). A similar relationship holds for egg masses of the noctuid *Spodoptera litura* (Fab.). This moth deposits its eggs in multilayered, scale-covered masses (Braune, 1982). Layering of eggs in masses is common among lepidopteran species whose egg masses are attacked by parasitoids. Given the physical constraints on stacking design and egg shape, the question of optimal design for a given egg mass number can be phrased as: how many layers of what numbers and arrays of eggs hide the greatest percentage of eggs?

Models

MODEL 1: The problem of minimizing the percentage of exposed eggs is equivalent to minimizing the surface area of a geometric solid relative to its volume. Using a truncated cone as a geometrical model, one can calculate the optimal height relative to the basal radius by minimizing exposed surface area (sides and top) relative to volume. The number of layers an egg mass should have for a given clutch size can be predicted from this model (Fig. 1). The optimal shape for this model when translated into eggs is such that there should be as many layers of eggs as there are eggs in an average radius of the basal layer.

MODEL 2: Theoretical egg masses can also be generated by stacking successively smaller egg layer arrays on a basal layer (stacking of each egg onto the triad of eggs beneath it, with no overhanging eggs). Such a mass would take on the shape of a pyramid with as many sides as there were line segments formed by eggs in the circumference of the basal layer. The ideal shape for the basal layer would be a circle since this shape minimizes the circumference relative to the inscribed area. The best hexagonal approximation to a circle is a hexagon (for those with 2-7 eggs on a side) or a rounded hexagon (with a few eggs centered on each face; 8 eggs on a side and larger). Optimally built egg masses would appear as six-sided, miniature, truncated pyramids, flat-topped with steep (60 degree) sides, with the number of layers of eggs dependent on the clutch size. The number of layers giving the smallest percentage of exposed eggs (highest % hidden) should roughly be equal to the number of eggs on their respective basal sides, since the sides contain the same numbers of eggs as their respective radii (from the first model).

Table 1 shows the percentage of eggs hidden in a mass for a given base layer array, for 6 such layers in masses composed of fewer than 1000 eggs. Owing to the stacking design (it is not space-filling), these pyramidal masses overestimate the number of optimal layers relative to the model using a truncated cone, for a given base size (compare "best percentages" numbers of layers with regard to number of eggs on a basal side).

Discussion

Table 1 shows that for egg masses totalling less than 1000 eggs and up through 6 layers, more than half the eggs can be hidden in those masses which have from 5 to 11 eggs on a basal (hexagonal) side, and this can be achieved if the eggs are stacked in more than 2 layers for masses starting with 7 on a side. The best design for smaller masses is to have about the same number of layers as there are eggs on a side. Egg masses which only have one layer hide no eggs, even though the more central eggs are somewhat less exposed.

Consider the question: if one could restack eggs after a given number were deposited, when, by adding another egg to a mass, does it become more profitable to add another layer (considering the whole range of fixed egg mass sizes)? The minimum number of eggs necessary to hide one egg in a mass is 10, so that it becomes more profitable at 9 eggs to add a tenth so that the mass forms 2 layers than add the tenth egg in a single layer.

Table 1. The number of eggs, number and percent hidden eggs (maxima), for masses based on hexagonally-shaped bottom layers, by number of layers.

i = number of eggs on a side of hexagonally-shaped basal layer
l = number of layers
n = number of eggs in mass
h = number of eggs hidden
% = percentage of eggs hidden
* = best percentage for a given base

i	l	n	h	%
2	2	10	1	10.0*
3	2	31	7	22.6
	3	37	10	27.0*
	4	41	11	26.8
4	2	64	19	29.7
	3	82	31	37.8
	4	92	37	40.2
	5	101	41	40.6*
	6	105	42	40.0
5	2	109	37	33.9
	3	145	64	44.1
	4	170	82	48.2
	5	185	92	49.7
	6	201	101	50.2*
6	2	166	61	36.7
	3	226	109	48.2
	4	272	145	53.3
	5	305	170	55.7
	6	326	185	56.8
7	2	235	91	38.7
	3	325	166	51.1

	4	398	226	56.8
	5	455	272	59.8
	6	497	305	61.4
8	2	316	127	40.2
	3	442	235	53.2
	4	548	325	59.3
	5	635	398	62.7
	6	704	455	64.6
9	2	409	169	41.3
	3	577	316	54.8
	4	722	442	61.2
	5	845	548	64.9
	6	947	635	67.1
10	2	514	217	42.2
	3	730	409	56.0
	4	920	577	62.7
11	2	631	271	42.9
	3	901	514	57.1
12	2	760	331	43.6
13	2	901	397	44.1

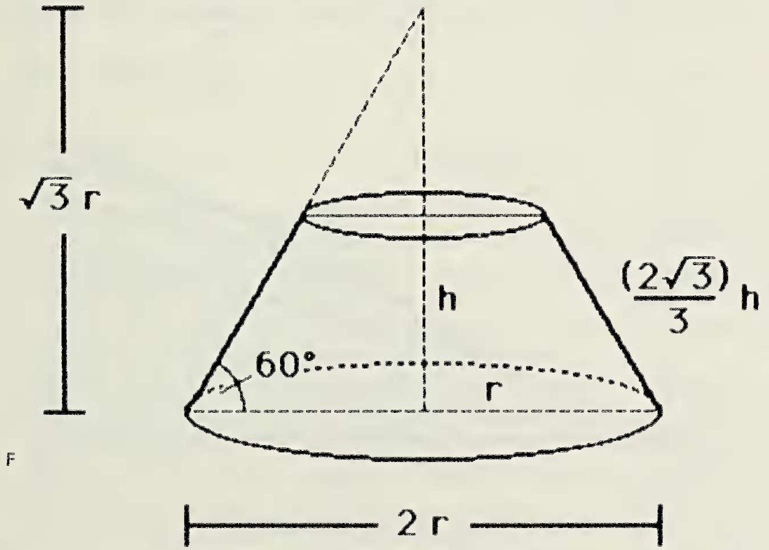

Fig. 1. Geometrical model of an egg mass by a 60 degree truncated cone (the same lateral angle produced by tetrahedral packing), with basal radius (r) and height (h).

By plotting the percentage of eggs hidden against egg mass size, for each set of masses consisting of from 2 to 6 layers from Table 1, one can roughly see the trade-off values at which successive pairs of curves cross (Fig. 2). These crossover values are the minima at which additional layers become more profitable when adding a single egg. They are, approximately: 19 (by adding one egg, rearrange from 2 layers into 3 layers at approximately 19 eggs), 67 (3 to 4), 160 (4 to 5), and 265 (5 to 6). An egg mass of 100 eggs should have 4 layers.

Most insects that deposit batches of eggs in excess of 100 per clutch do not deposit them in multi-layer masses. Among these batch-layers, few deposit their eggs in situations where the eggs are more or less exposed to the air and parasitoids. Females of the lasiocampid *Malacosoma americanum* (Fab.) produce a covering (besides eggs) for their exposed eggs (Darling and Johnson, 1982). The modelling presented in this paper probably only applies to a handful of species that for one reason or another are constrained to deposit their egg masses in very exposed situations and which do not guard their eggs or protect them using some other means. One species satisfying these criteria is the nymphalid *Asterocampa clyton* (Boisduval & Le Conte).

Notes on *Asterocampa clyton* Egg Masses

A. clyton deposits its eggs in large, naked, pyramidal clusters (Riley, 1874; Edwards, 1876). Roughly 2 out of every 3 egg masses of this butterfly

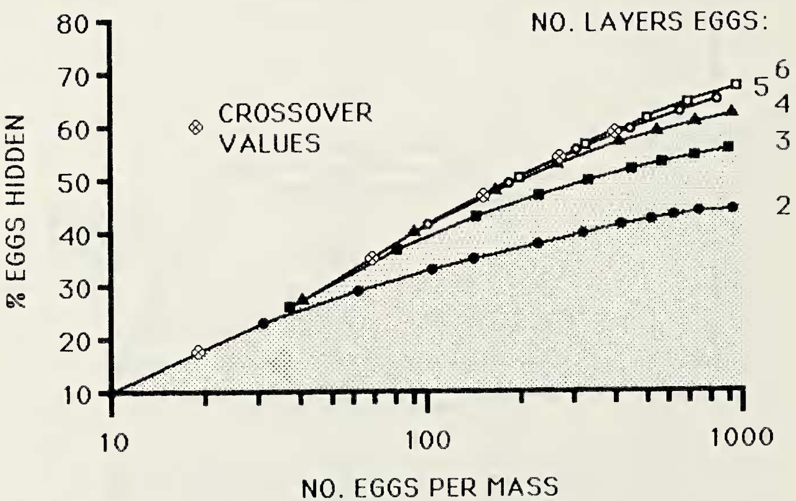

Fig. 2. Plots of the percent eggs hidden, by egg mass size, for up to 6 layers of eggs (generated from Table 1), showing the crossover values of mass size at which there is an advantage to an additional layer of eggs.

are to some degree parasitized by scelionid wasps (Friedlander, pers. obs.). From about 50 to 200 of the exposed eggs in the masses are routinely parasitized yielding levels of parasitism of over 90% in small masses to about 40% in very large masses. More than one female scelionid probably account for some of the high parasitism observed in large masses.

Table 2 shows data for egg masses of *Asterocampa clyton* compared with values predicted by modelling. Only 8 masses in the author's collection were suitable (no parasitism, or parasites/larvae not emerged) for constructing the table. Egg masses of this and a related species (*A. idyja argus* (Bates)) are known to have up to 7 layers (Friedlander, pers. obs.). The egg mass design of *Asterocampa clyton* compares favorably with predictions from the egg-stacking models.

Table 2. Egg mass size and shape of *Asterocampa clyton* as compared with predicted design.

Size (n)	**No. hidden**	**No. layers (obs./exp.)**	**% hidden (obs./exp.)**
61	15	2/3	25/51
74	23	2/3	31/52
93	32	4/4	34/40
115	31	4/4	27/43
139	54	4/4	39/45
193	86	4/5	45/60
214	85	5/5	40/50
217	100	4/5	46/51

Conclusions

The composite model presented here should be applicable in all cases where clusters of a sessile life stage are subject to mortality factors affecting only the exposed (and not the hidden) units. Among the Lepidoptera the model would apply in cases where eggs were deposited in exposed masses and these eggs were subject to differential mortality based on their relative positions in the mass (exposed, hidden).

The data from the few egg masses of *A. clyton* compare favorably ($y = 79.37 - 0.11x$, $r^2 = 0.76$, $n = 8$) with those obtained by Braune (1982) for *Spodoptera litura* ($y = 76.23 - 0.07x$, $r^2 = 0.71$, $n = 39$), comparing percentage of exposed eggs with the number per mass. Statistical tests (alpha (2-tailed) = 0.05) of differences in both slope ($t = -0.81$, d.f. = 43, $p > .43$) and elevation ($t = -0.78$, d.f. = 44, $p > .44$, $p > .45$) of these regression lines resulted in no statistically significant differences being found. Braune (1982) noted that 54% of the egg batches he studied were parasitized. Small clutches were 40-100% parasitized while large clutches experienced much lower levels of less than 50% parasitism (y = 97.04 - 0.11x, r^2 = 0.55, n= 35). The noctuid moth might be responding in the same way to parasitism as the butterfly, notwithstanding the covering of scales for its eggs.

The packing design, shape and size of the basal layer of eggs, the number, shapes and sizes of additional layers, all have an effect on the percentage of eggs exposed to mortality factors, and are therefore potentially subject to modification by natural selection. Change in the shape of egg masses is but one possible response, perhaps an unusual one among the Lepidoptera.

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